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NEWS AND VIEWS

PERSPECTIVE

Catadromous eels continue to be slippery research subjects

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As adults, Atlantic eels (*Anguilla rostrata* in the Americas and *Anguilla anguilla* in Europe) are tubular slime-covered fish that spend most of their catadromous life cycle in coastal environs before swimming far out to sea to reproduce, as part of an intergenerational migratory circuit that provides an interesting reversal of the pattern displayed by adult anadromous salmon that live mostly in the ocean but then migrate long distances to spawn in freshwater streams. Earlier genetic findings on Atlantic eels involved specimens collected across their broad continental ranges and generally indicated that conspecifics probably engage in panmictic or quasi-panmictic spawning, from which arise leaf-shaped leptocephalus larvae that then disperse back to coastal locations more or less at random with respect to the widespread geographical origins of the parental genes they carry. In this issue, Als *et al.* (2011) add exciting information about this peculiar life-history pattern of catadromous Atlantic eels by extending the genetic analyses to eel larvae collected from the Sargasso Sea, the oceanic area where both species spawn. Results help to confirm standard textbook wisdom that these catadromous eels are nearly unique in the biological world by having both broad geographical distributions and yet displaying intraspecific near-panmixia.

Keywords: hybridization, mating patterns, microsatellites, phylogeography, population structure

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History of indirect mating evidence from continental samples

The history of research on reproduction by catadromous Atlantic eels has been a history of inferences and deductions based mostly on indirect evidence (Aida *et al.*, 2003; Avise, 2003), because no one has ever actually observed eel spawning in nature. Indeed, no one has even seen adult

eels within thousands of kilometres of their spawning site in the Sargasso Sea, an expansive region in the tropical western Atlantic Ocean (Fig. 1). So, how do researchers know about this spawning location and about the mating behaviours of the eels within it?

The story begins in the 1920s with the efforts of Johannes Schmidt (1922, 1923, 1924) who trawled plankton nets across the North Atlantic in search of the tiny leptocephalus eel larvae (Fig. 2) that would be the signatures of recent spawning events. Schmidt and many other researchers that followed his lead (e.g. Boëtius 1980; McCleave

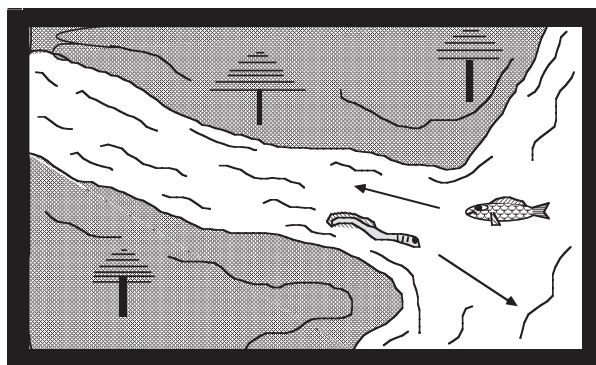


Fig. 1 Catadromous adult eels undergo long spawning migrations from coastal streams to oceanic realms, whereas anadromous adult salmon do quite the reverse, as summarized in this limerick by JCA:

For an eel, the ideal strategy
Is to grow in a stream, mate at sea.
But a salmon's sweet dream
Is to spawn up a stream,
Using reverse psychology!

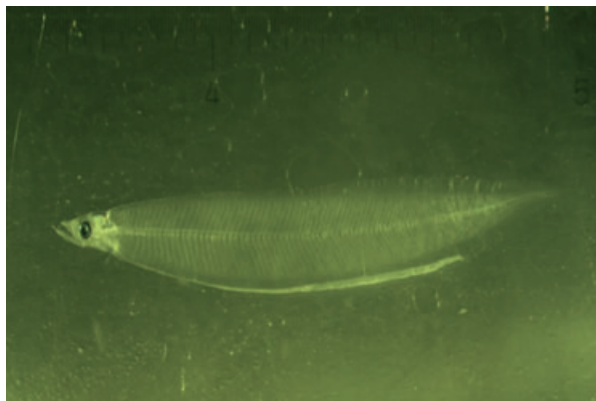


Fig. 2 Leptocephalus eel larva collected in the Sargasso Sea (photograph: Peter Munk).

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et al. 1987) mapped the highest densities of the smallest and youngest eel larvae to particular regions of the Sargasso Sea, and thereby deduced where spawning must take place in each of the two North Atlantic species (whose larvae differ morphotypically in numbers of vertebral myomeres).

The research saga entered an entirely new phase in the 1970s with the introduction of molecular markers (allozymes, initially) to eel population biology (Koehn 1972; Koehn & Williams (1978). For example, George Williams and Richard Koehn (1984) and their colleagues found only weak spatial genetic structure among widespread geographical populations of *Anguilla rostrata* in North America (Williams *et al.* 1973), as did other researchers for adult populations of *A. anguilla* in Europe (de Ligny & Pantelouris 1973; Rodino & Comparini 1978). Such results generally were interpreted as consistent with genetic panmixia within each species followed by the random dispersal of larvae back to various sites on their respective continental mainlands.

In the mid-1980s, my colleagues and I added mitochondrial (mt) DNA to the emerging story by surveying adult eels from sites spanning Maine to Louisiana (Avisé *et al.* 1986). Given our prior experience in documenting dramatic mtDNA population structure in various fishes (e.g., Bermingham & Avisé 1986) and many other vertebrate and invertebrate animals (early reviews in Avisé 1986; Avisé *et al.* 1987), we fully expected to find strong genetic differentiation among populations of *A. rostrata* as well, and thereby become rich and famous by demolishing the standard dogma about eel panmixia. So, we were both surprised and somewhat chagrined when even our powerful mitochondrial markers uncovered little or no spatial genetic heterogeneity in *A. rostrata*. Later, similar paucities of geographical variation in mtDNA (Lintas *et al.* 1998), and to a considerable extent in polymorphic nuclear microsatellites (Daemen *et al.* 1997; Wirth & Bernatchez 2001; Mank & Avisé 2003), likewise were documented for many populations of *A. anguilla* in Europe, although Wirth & Bernatchez (2001) observed geographical patterns interpreted as evidence against panmixia (but not confirmed in the present study by Als *et al.*). In contrast to the spatial genetic uniformity *within* each eel species, all of these as well as several other classes of molecular markers (Salvadori *et al.* 1997; Nieddu *et al.* 1998; Lehmann *et al.* 2000) proved to distinguish *A. rostrata* from *A. anguilla* readily, thus confirming earlier suspicions based on morphology that two mostly separate gene pools of eels co-reside in the North Atlantic Basin.

Towards more direct mating evidence from the spawning grounds

Although the current study by Als *et al.* (2011) is not the first to extend genetic analyses to larval eels from the oceanic spawning arena (see Comparini & Rodino 1980), it is by far the most ambitious such molecular survey to date. The new genetic data not only confirm quite directly that

two gene pools coexist in the Sargasso Sea, but they also refine our understanding of how those separate gene pools are spatio-temporally arranged at the key reproductive phase of the eel life cycle.

The authors' findings are noteworthy in some other regards as well. It has long been suspected from genetic and other evidence that *Anguilla rostrata* and *Anguilla anguilla* hybridize at least occasionally and, incredibly, that some of the adult hybrids end up in Iceland (Williams *et al.* 1984; Avisé *et al.* 1990; Albert *et al.* 2006), an island about halfway between North America and Europe. Exactly how this comes about remains an enduring mystery, but the current genetic survey by Als *et al.* (2011) adds at least two important pieces of information. First, the authors genetically document one larval F1 hybrid, thereby providing direct confirmation of interspecific spawning in the Sargasso Sea. Second, the new microsatellite data overall appear to diminish the possibility that hybridization and introgression are extremely common phenomena across the broad geographical zone of overlap between the oceanic spawning regions of these two species.

Looking forward

Many questions remain to be answered before we can fully claim to understand the ecology and evolution of the marvellous life cycles of catadromous eels. Personally, I think that some of the most intriguing open issues have to do with mechanistic intersections between the mating and migratory behaviours themselves. For example, how and how often do genetically intermediate specimens (i.e., F1 and perhaps backcross or later-generation hybrids) come to occupy geographically intermediate locations (e.g., Iceland)? Eventually, eel researchers will have to come to grips with this and many other such slippery issues.

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The author is interested in molecular ecology and evolution.

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